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Towards the reconstruction of subfossil vegetation: an unexpected plant record in Early Holocene sediments of a mire in NE Poland

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We reconstructed a subfossil plant community, *Sphagnum* sect. *Acutifolia-Carex*, in the development of Borki mire located in NE Poland. The plant community existed in the Early Holocene, from the Preboreal until the middle of the Boreal periods. We found a co-occurrence of both ombrotrophy/oligotrophy and minerotrophy plant taxa indicators, as well as an intriguing concomitance of them with different preferences for acidity and moisture of the substratum. Statistically significant, non-random, positive associations were determined for several pairs of species where such dyads were formed by taxa typical of different habitats. Such a combination of taxa has not been reported, and hence this community does not have many equivalents in subfossil or modern phytocoenosis. Its occurrence at the studied mire supposedly resulted from specific local hydrological conditions during the Early Holocene.

Introduction

The diversity of peatland vegetation is shaped by several environmental factors, such as pH and base-richness, moisture-aeration regime, and distance from the upland mineral soil (Sjörs 1948, Økland 1990, Rydin and Jeglum 2008). Undoubtedly, these factors also affected the vegetation forming in the past. Reconstruction of long-term succession of subfossil mire phytocoenoses is possible by using the plant macroscopic remains analysis. This is due to several advantageous features of macrofossils for the reconstruction of vegetation and the palaeoenvironment. First, plant macroscopic remains found in biogenic sediments, especially in peat, can be identified at the species level, more often than pollen and spores. In addition, species that are not represented by pollen are also present (e.g. mosses). A further advantage of plant macrofossil analysis is the possibility to recognize local flora and vegetation, owing to the specific nature of the sedentation process.

The understanding of the importance of plant macrofossil analysis and appropriate interpretation of results are possible owing to the fact that every remain is treated as evidence that an organism lived not in isolation, but in association with other organisms (Spicer 1989). Such an assumption is applied in the so-called community and assemblage approach, which explores the interspecific relationships (plant sociology) of plant taxa occurring together at a site (Schepers *et al.* 2013).

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As we know, plant assemblages have changed in the past and therefore, these modern assemblages differ fundamentally from those over the past 300 million years (see Lyons *et al.* 2016). However, according to Jackson and Williams (2004), a characteristic feature of the Quaternary is that fossil floras (also faunas) are similar or identical to modern biota, and most Quaternary biota have modern counterparts. Accordingly, knowledge about living organisms and communities can be applied directly to the interpretation of the Quaternary fossil record. In the case of Late Glacial and Holocene plant macrofossil assemblages, the possibility to match them with modern vegetation analogues is even more tangible (Birks 1993). However, the persistence of particular species assemblages at any site for more than a few thousand years is rare (Jackson and Overpeck 2000). Macrofossil data show that changes in vegetation may arise from the abundance of plant taxa at the site, as well as the invasion and extinction of species (Jackson *et al.* 1997, Weng and Jackson 1999). In principle, the postglacial plant communities are considered to have contemporary analogues, located geographically further. Such geographical shifts in vegetation were usually north-south, and occurred in response to postglacial changes in temperature and moisture (Huntley and Birks 1983). The specific order in which past vegetation functioned was often reflected also in the pattern of local succession. The first sequence discerned on the mineral substratum was typically tall-sedge phytocoenoses gradually leading to bogs or transitional mires overgrown by thickets or forests. In this paper, we present vegetation combining minerotrophic and ombrotrophic elements. Their coexistence was confirmed by co-occurrence analysis. Thus, the aims of our article are: (1) to show reconstructed subfossil vegetation; (2) to point out intriguing plant taxa compositions; and (3) to determine the possible reasons for their occurrence at the studied site.

Study Area

The study area is located in northeastern Poland, in the Knyszyńska Forest Landscape Park (Fig. 1). Local relief was formed by the Saalian glaciation (Musiał 1992), which produced a number of glaciofluvial features that include kames, kame terraces, and numerous melt water forms. However, the immediate neighbourhood of the Weichselian glaciation landscape results in Holocene sediments filling river valleys and melt depressions. The Knyszyńska Forest occurs in the vicinity of the Vistula and Nemunas rivers watershed. The study site has a transitional temperate climate. The mean annual temperature is 7°C and the monthly averages range between –4°C in January and 18°C in July (Sasinowski 1995). The annual precipitation is 570 mm. The characteristic feature of vegetation is the presence of *Picea abies* in nearly all forest communities, and an absence of *Fagus sylvatica*.

The mire under study, Borki is located in the eastern part of the Park, and has been protected since 1990 as a nature reserve. The Borki mire developed in a large meltwater basin and occupies almost 287 ha. Its altitude varies between 130–136 m a.s.l. From the east, it borders a plateau enclosed by kame terraces. At the western margin of the Borki mire runs the Sokołda river, separated from the mire by a 300 m-wide zone of mud and alluvium. The mire is soligenous, irrigated by waters from deeper water-bearing horizons, underlain by a clay layer (Dembek 1993). Vascular plants found here include *Betula pubescens*, *Betula humilis, Carex chordorrhiza*, *Carex lasiocarpa*, *Carex rostrata*, *Drosera rotundifolia*, and orchid *Liparis loeselii*. Moss flora is also rich, with *Hamatocaulis vernicosus*, *Paludella squarrosa*, *Helodium blandowii*, *Tomentypnum nitens*, *Sphagnum girgensohnii Sphagnum squarrosum*, and *Sphagnum palustre* (Żarska 1993). Mire is forested by *Carici chordorrhizae-Pinetum*, *Sphagno girgensohnii-Piceetum* and, in the location of studied core, by *Thelypterido-Betuletum pubescentis* (Czerwiński 1995).

Materials and methods

Field work and laboratory analyses of peat

A sediment core (coded as BIII core; Fig. 1) was collected to a thickness of 480 cm using an Instorf peat corer (Russian drill) with a length of 50 cm and a width of five cm. GPS coordinates for the drill point are: 53°13′2′′N, 23°28′37′′E,

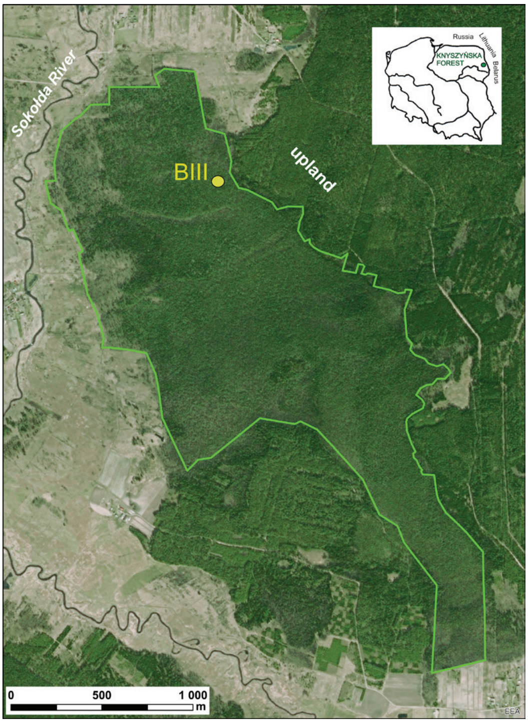


Fig. 1. Location of the Borki mire and BIII drilling.

138.7 m a.s.l. The peat core was packed in plastic half-cylinders and plastic film. In the laboratory, sediment samples were taken at 5 cm intervals. At first, analyses were performed for samples every 10 cm (Drzymulska 2006a, 2008), while the remaining material was frozen. The first obtained results showing an interesting palaeobotanical record gave reasons to undertake further work with the remaining material. Altogether 96 samples were analyzed.

Sediment from each re-frozen sample was used for more detailed analyses of plant macrofossils. Peat was boiled in water with the addition of 10% KOH and then washed through a 0.2 mm sieve. Seeds and fruits were picked, and placed in a glycerine-thymol mixture, and then studied using a stereoscopic microscope at a magnification of 10–100×. Vegetative plant remains (roots, epidermis, periderm, rhizoderm, leaves and stems, wood) were identified with a light microscope at 200–400× magnification. The moss nomenclature follows Ochyra *et al.* (2003) and the vascular plant nomenclature Mirek *et al.* (2002). For unidentified brown mosses, Bryales term was used. The remains were identified with the help of Grosse-Brauckmann (1972, 1974), Katz *et al.* (1977), Mauquoy and van Geel (2007), and the collection of macroscopic plant remains at the Institute of Biology, University of Bialystok. The name *Sphagnum fuscum*/*rubellum* was used due to the difficulty of distinguishing *Sphagnum fuscum* from *Sphagnum rubellum* in the fossil state, particularly in the case of a lack of stem leaves, as noted by Tuittila *et al.* (2007) and Gałka and Lamentowicz (2014). The botanical composition was estimated with an accuracy rounded to 1% based on the proportion of each taxon's vegetative remains in the total tissue mass. Generative remains were counted. Ecological values were used after Ellenberg (1974), Ellenberg *et al.* (1992) and Zarzycki *et al.* (2002). These indicator value scales correspond to each other: the value 5 according to Zarzycki *et al.* (2002), for instance, corresponds to Ellenberg's value 9–10.

In total, four selected samples of peat were dated in the Gliwice Radiocarbon Laboratory (GdA). This was based on the knowledge that bulk sediment can lead to acceptable age estimates in the case of different types of peat deposits, for example, organic-minerogenic deposits of fen-type peat mire (Margielewski *et al.* 2011), poor fen (Fiałkiewicz-Kozieł *et al.* 2014) or basal peats (Holmquist *et al.* 2016). OxCal ver. 4.2.3 online software (Bronk Ramsey 2013) was used to calibrate the radiocarbon age of the samples. Based on the ^{14}C dates and with use of the Depth/Age software (Walanus and Nalepka 2015), the age-depth model for the analyzed profile was constructed. Chronology for the Holocene was used according to Mangerud *et al.* (1974), with calibration of chronozone boundaries by Walanus and Nalepka (2010). The diagram of plant macrofossils was constructed with the software package POLPAL (Nalepka and Walanus 2003). Macrofossils were ordered according to the weighted average of their depths/ages.

Statistical methods

Statistical data analysis was conducted using the cooccur package (ver. 1.3; Griffith *et al.* 2016) for R environment (ver. 3.4.3; R Core Team 2017). This package constitutes an extended R implementation of a probabilistic model for analyzing

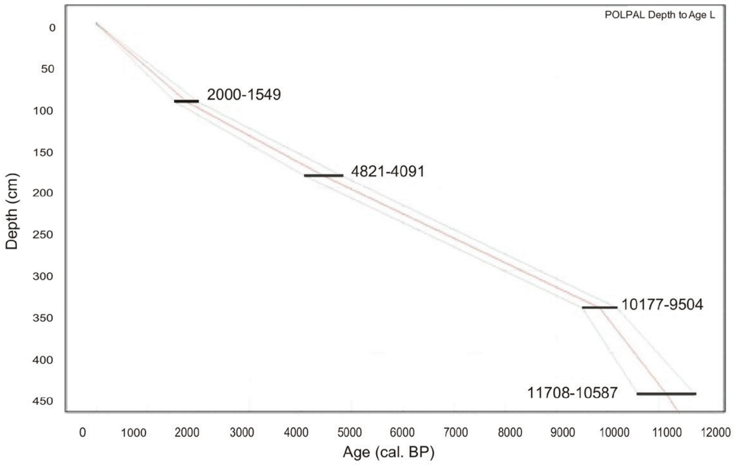


Fig. 2. Age-depth model for the BIII profile.

species co-occurrence patterns proposed by Veech (2013). The null model assumes independence and randomness. Veech (2013) originally utilized a combinatorial approach, which was retained by Griffith *et al.* (2016) as an option, but supplemented it with a hypergeometric alternative.

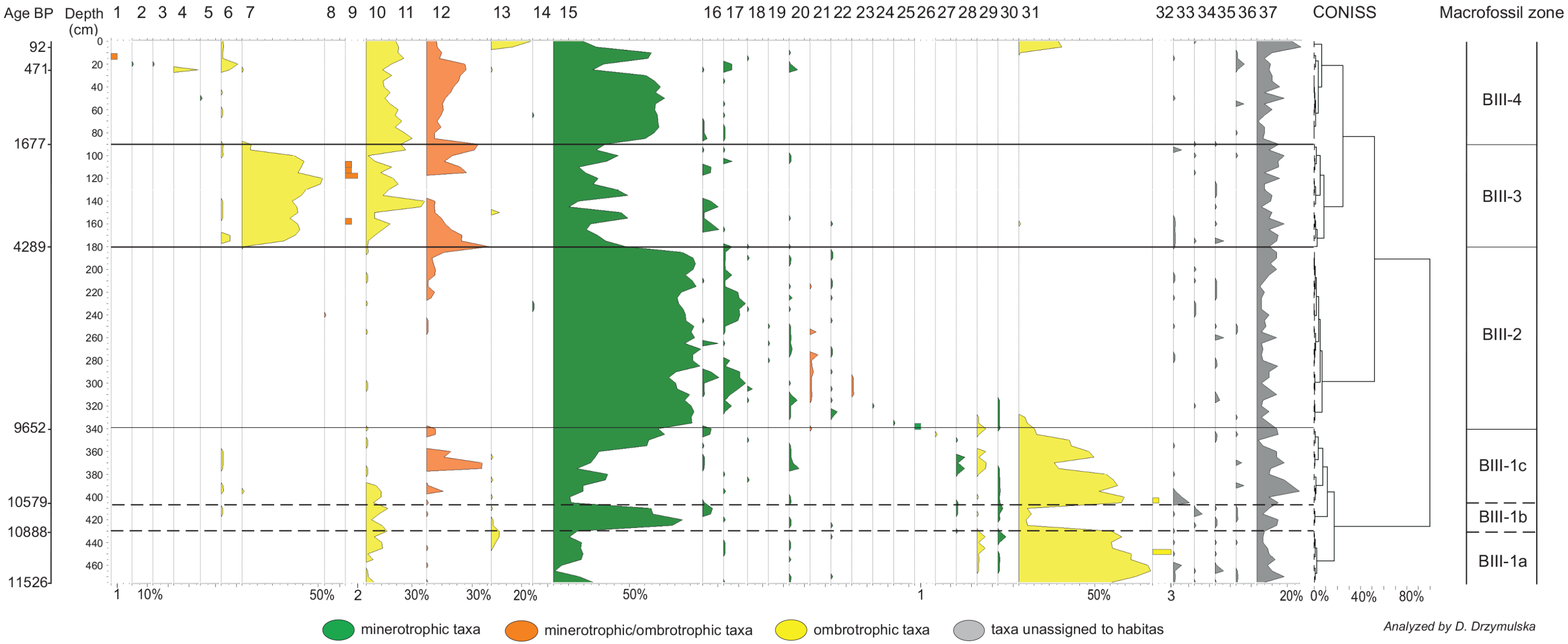
Since the main function, "cooccur()", accepts presence-absence data, original abundance values (percentages or, in the case of generative remains, counts) were converted into a binary (0/1) form. We used a package-default species-by-site layout, where sites (columns) were represented by consecutive five-centimeter-long sections of the peat core. The paramount part of a "cooccur()" output comprised probabilities for classifying negative and positive associations, calculated using the hypergeometric distribution. According to Griffith *et al.* (2016), these probabilities could be interpreted as *p* values. The standardized effect size was defined as the difference between the expected frequency of co-occurrence and its observed counterpart, divided by the number of sampling sites (core sections here). Its magnitude can vary from –1.0 (perfect negative association) to 1.0 (perfect positive association). All species pairs characterized by very low expected co-occurrences (< 1; i.e., expected to share less than a single core section) were removed from the output listing. Moreover, the upper (inclusive) acceptable deviation-from-expected threshold for the truly random associations was set at 0.1 × *N*, where *N* stands for the total number of core sections. Such a value was suggested by Griffith *et al.* (2016), based on a power analysis reported by Veech (2013). Both critical values were utilized by default by the "cooccur()" function of the cooccur package ("thresh = TRUE" and "true_rand_classifier = 0.1" respectively).

The macrofossil zones were recognized based on the taxonomic composition of peat samples, supported by stratigraphically constrained cluster analysis (CONISS; Grimm 1987) using POLPAL software (Nalepka and Walanus 2003). To determine the significant number of such zones (i.e., validate the above procedure performance), the stratigraphically constrained hierarchical cluster analysis had been recreated using the vegan (ver. 2.5-4; "vegdist()" function) and rioja (ver. 0.9-15.1; "chclust()" function) packages for R (Oksanen *et al.* 2019, Juggins 2017, respectively). The resulting scree plot was subsequently contrasted with the broken-stick model ("bstick()" function from rioja package). The adopted number of zones corresponded to the largest integer for which the sum of squares remained (unchangingly) higher than the corresponding expectation based on the broken-stick model (Bennett 1996, Stephens *et al.* 2012).

Results

Plant macrofossils and past vegetation

The age of the oldest peat sample, determined based on radiocarbon dating (Table 1) and the



1 - *Carex* sect. *Paniculatae* - nuts, 2 - *Sphagnum* sect. *Subsecunda*, 3 - *Warnstorfia* cf. *exanulata*, 4 - *Pleurozium schreberi*, 5 - *Tomentypnum nitens*, 6 - Ericaceae - roots, 7 - *Sphagnum magellanicum*, 8 - *Menyanthes trifoliata* - epiderm, 9 - *Menyanthes trifoliata* - seeds, 10 - *Pinus sylvestris* - periderm, 11 - *Sphagnum palustre*, 12 - *Sphagnum* sect. *Cuspidata*, 13 - *Drepanocladus* sp., 15 - *Carex* sp. - radicles, 16 - *Phragmites australis* - epiderm, 17 - Bryales, 18 - Cypearceae - epiderm, 19 - *Eriophorm angustifolium* - epiderm, 20 - *Thelypteris palustris* - tissues, 21 - *Scheuchzeria palustris* - epiderm, 22 - *Alnus* cf. *glutinosa* - periderm, 23 - *Carex* cf. *limosa* - radicles, 24 - *Meesea triquetra*, 25 - *Scutellaria galericulata* - epiderm, 26 - *Carex riparia* - nuts, 27 - *Andromeda polifolia* - leaf epiderm, 28 - *Sphagnum teres*, 29 - *Polytrichum strictum*, 30 - *Equisetum fluviatile* - rhizome epiderm, 31 - *Sphagnum fuscum*/*rubellum*, 32 - *Betula nana* - nuts, 33 - *Betula* sp. - periderm, 34 - *Salix* sp. - periderm, 35 - deciduous wood, 36 - *Sphagnum* sp., 37 - unidentified plant remains

Fig. 3. Diagram of plant macrofossils.

age-depth model (Fig. 2), was connected with the beginning of the Preboreal period. The analyzed core was composed of peat consisting of generally well-preserved plant remains. The share of unidentified tissue matter amounted to less than 30%, usually about 5–10%. Most of the peat material comprised vegetative remains such as tissues of vascular plants and remains of mosses - leaves, branches and stems. Fruits and seeds were found sporadically. The remains of 33 plant taxa were identified (Fig. 3).

The quantitative representation of major plant types is as follows: trees and shrubs — four taxa, dwarf shrubs — three, herbs — ten, pteridophytes — two, peat mosses — seven, and brown mosses — seven. Three of the taxa are not found in the Knyszyńska Forest at the present time. These are *Betula nana*, *Scheuchzeria palustris* and *Meesea triquetra*.

From the present trophic preferences point of view, we noted a simultaneous presence of both typical indicators of ombrotrophy/oligotrophy and indicators of minerotrophy. Peat mosses from *Acutifolia* section, recognized as *Sphagnum fuscum*/*rubellum*, as well as *Polytrichum strictum*, *Andromeda polifolia*, Ericaceae dwarf shrubs, and *Betula nana* belonged to the first group, whilst *Equisetum fluviatile*, *Sphagnum teres*, *Thelypteris palustris*, *Scutellaria galericulata*, *Alnus* cf. *glutinosa* and *Carex* sp., including *Carex riparia,* represent the latter. The co-occurrence of ombrotrophic and minerotrophic species was confirmed by the finding of statistically significant, non-random, positive associations between species contemporarily representing different types of mires. In the scale of the whole BIII core, intriguing co-occurrences were noted for eight taxa pairs: *Sphagnum fuscum*/*rubellum* and *Equisetum fluviatile*, *Polytrichum strictum* and *Equisetum fluviatile*, *Sphagnum fuscum*/*rubellum* and *Sphagnum teres*, *Polytrichum strictum* and *Sphagnum teres,* Ericaceae and *Sphagnum palustre*, *Sphagnum* sect. *Cuspidata* and *Equisetum fluviatile*, *Sphagnum magellanicum* and *Sphagnum palustre* and also *Sphagnum magellanicum* and *Menyanthes trifoliata* (Fig. 4).

Four main macrofossil zones were distinguished from the Early Holocene to the present (Fig. 3) through stratigraphically constrained cluster analysis. The first, basic dividing line was drawn at a depth of 340 cm, and macrofossil zone BIII-1 was delimited. The next zone limits were identified at 190 cm (between) and 105 cm (between the zones BIII-2 and BIII-3, and BIII-3 and BIII-4, respectively). The BIII-1 zone was further divided into three subzones: BIII-1a, BIII-1b and BIII-1c. Importantly, the above number of reliably recognizable major macrofossil zones (four) also resulted from contrasting the empirical data with the broken-stick model (Fig. 5; see also Materials and Methods section). The characteristics of particular macrofossil zones were as follows:

Zone BIII-1, 480–340 cm, 11526–9652 cal. BP. This zone is characterized by the predominance of *Sphagnum fuscum*/*rubellum* and *Carex* sp. remains. *Polytrichum strictum, Thelypteris palustris* and *Equisetum fluviatile* occurred frequently, as well as tree/shrub tissues (*Pinus sylvestris*, *Betula* sp., *Betula nana*, *Salix* sp., deciduous wood). In the lower part, assigned as subzone BIII-1a, *Sphagnum fuscum*/*rubellum* leaves were the most abundant component. The transition to the overlying subzone BIII-1b marked the peak of *Carex* sp. remains, while the BIII-1c subzone marked the re-domination of *Sphagnum fuscum*/*rubellum*, accompanied by *Sphagnum*

Table 1. Radiocarbon dating of sediments from Borki III profile. BP = before present, cal. BP = calibrated years before present.

Core/Depth (cm)	Material	No. Lab	C^{14} date BP	Age cal. BP (95% probability)
BIII/95	peat	Gd-15646a	1850 ± 100	2000–1549
BIII/185	peat	Gd-15634	3960 ± 120	4821–4091
BIII/345	peat	Gd-15636	8720 ± 140	10177–9504
BIII/450	peat	Gd-30056	9730 ± 170	11708–10587

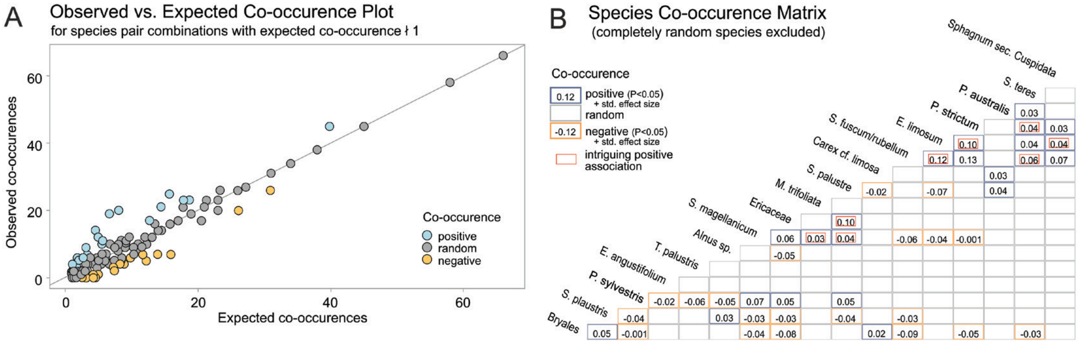


Fig. 4. Species co-occurrence data visualization; (**a**) observed-expected scatterplot and (**b**) association matrix showing directionality, standardized effect sizes, as well as their statistical significance

palustre. The rate of peat accumulation in these three subzones was 0.78 mm/year (BIII-1a), 0.65 mm/year (BIII-1b) and 0.75 mm/year (BIII-1c).

Zone BIII-2, 340–180 cm, 9652–4598 cal. BP. This period involved a predominance of *Carex* sp. Among them *Carex* cf. *limosa* and *Carex riparia* were present. Bryales occurred commonly, as well as *Thelypteris palustris*. Tissues of *Scheuchzeria palustris*, *Phragmites australis* and tree/shrub remains appeared frequently. *Sphagnum palustre* was also observed. The rate of peat accumulation was 0.3 mm/year.

Zone BIII-3, 180–90 cm, 4598–2046 cal. BP. *Sphagnum palustre* and *Sphagnum magellanicum* occurred abundantly. Remains of *Carex* and *Pinus sylvestris* were numerous. The distinct presence of *Phragmites australis* epiderm and Ericaceae roots was described. Tissues of trees/shrubs were still present. The rate of peat accumulation was 0.34 mm/year.

Zone BIII-4, 90–0 cm, 2046 cal. BP–Present. Compared to the previous phase, the almost total disappearance of *Sphagnum magellanicum* was noted. *Carex* sp., *Sphagnum palustre* and *Pinus sylvestris* were dominant. Ericaceae, *Phragmites australis* and Bryales remains accompanied them. In the upper layer of peat, leaves, stems and branches of *Sphagnum fuscum*/*rubellum* and *Sphagnum* sect. *Cuspidata* appeared. The rate of peat accumulation was 0.53 mm/year.

The above zones were the basis for the reconstruction of subfossil plant communities. For the BIII-1 zone the phytocoenosis was described as *Sphagnum fuscum*/*rubellum*-*Carex* community, for the BIII-2 zone – as the low sedge-brown moss community, and for the zones BIII-3/BIII-4 — as the community of *Carex*-*Sphagnum* sect. *Sphagnum*-*Pinus*.

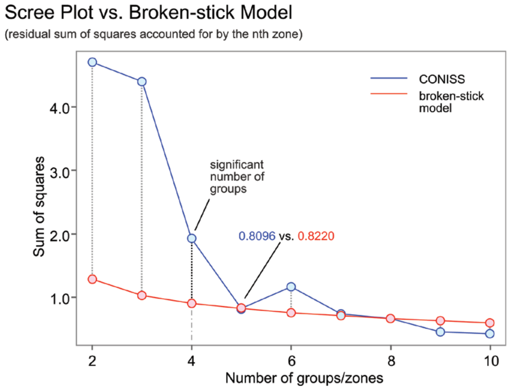


Fig. 5. Determination of the significant number of clusters/zones resulting from the stratigraphically constrained hierarchical cluster/zonation analysis using CONISS agglomeration method. The scree plot for said analysis is contrasted with the broken-stick model.

Statistical analysis of species co-occurrence

Of 435 species pair combinations, 274 pairs (63.0%) were removed from the analysis because the expected co-occurrence was below 1.0, and 161 pairs underwent further investigations (Fig. 4a). Statistically significant, non-random associations between species were found for 42 pairs (26.1%), and they were positive, denoting co-occurrence (as opposed to avoidance) for 22 of them (Fig. 4b). Although their effect sizes were significantly different from 0, they were not impressive, ranging between 0.02 and 0.13. Nevertheless, at least eight cases of positive associations were detected for pairs formed by taxa representing different habitats (Fig. 4b). It should be emphasized that application of this statistical method is rather novel in palaeobotanical studies, although the cooccur package is a concise, easy-to-use and powerful tool, offering a highly informative tabular output. Importantly, the method, which is rooted in a probabilistic model using the hypergeometric distribution, provides not only *p* values, but also standardized effect sizes with their directions.

Discussion

The knowledge on past mire environments can be broadened owing to searching and finding of similarities between present and past vegetation. This is based on the assumption that macrofossil assemblages are more or less analogous to any contemporary vegetational units in certain areas (Grosse-Brauckmann 1986). However, our results referring to the plant community existing at the beginning of the Preboreal period, in the vicinity of the BIII site, do not seem to fully support the above mentioned claim. The appearance of the interesting phytocoenosis (*Sphagnum fuscum*/*rubellum*-*Carex* community) and the onset of peat formation at the beginning of the Holocene, was the result from the development of peatland over previously less wet mineral ground. In such cases, the excessive accumulation of soil organic matter can lead to the formation of peatlands (Payette and Rochefort 2001) in wet topographic depressions, where the high water table promotes the growth of peat-forming plants (e.g. sedges and *Sphagnum* species) (Payette 2001). The origin of the studied mire at the beginning of the Preboreal period should be connected with factors stimulating the peat-forming process during the Early Holocene, such as the temperature increase, change of thermal balance in the ground, and permafrost disappearance (Żurek 1995). On the global scale, peatland formation of this kind seems to be more common than infilling (Rydin and Jeglum 2008). In northern Poland, however, peat formation is most frequently preceded by the lake phase, as reflected by the presence of lacustrine sediments in the deepest sediment layers. It is noted at least in Taboły and Kładkowe Bagno mires, located in the vicinity of the Borki site (Drzymulska 2006b).

Why was the initial community reconstructed in the BIII location recognized as intriguing? The ecological values referring to trophy and soil acidity for selected vascular plants forming subfossil community *Sphagnum fuscum*/*rubellum*-*Carex* are of wide range (from one to five), therefore confirming the specific character of this phytocoenosis: *Andromeda polifolia* (possible Ericaceae species) 1 (extremely poor soil) and 1 (highly acidic soils, pH < 4), *Betula nana* 2 and 1, respectively, *Alnus glutinosa* 3–4 and 4, *Equisetum fluviatile* 3–4 and 4–5, *Thelypteris palustris* 4-3 and 4 (Zarzycki *et al.* 2002). The rate of peat accumulation reaches intermediate values between those known for bog (0.9 mm/year) and fen peats (0.32–0.51 mm/year) (see Żurek 1986). This heterogeneity was confirmed by the discovery of six statistically significant, non-random, positive associations between species typically representing different types of present mires and connected with subfossil *Sphagnum fuscum*/*rubellum*-*Carex* community: 1) *Sphagnum fuscum*/*rubellum* and *Equisetum fluviatile*; 2) *Polytrichum strictum* and *Equisetum fluviatile*; 3) *Polytrichum strictum* and *Sphagnum teres*; 4) *Sphagnum fuscum*/*rubellum* and *Sphagnum teres*; 5) *Sphagnum* sect. *Cuspidata* and *Equisetum fluviatile;* and also 6) Ericaceae and *Sphagnum palustre*. Two statistically significant, non-random, positive associations were found for taxa co-occurring during the later stage of the mire development: *Sphagnum magellanicum* and *Sphagnum palustre* and also *Sphagnum magellanicum* and *Menyanthes trifoliata*.

Some of the above-mentioned pairs are not expected to co-occur based on the current ecological ranges of plant species. However, it should be emphasized that ecological preferences cannot be closed in a rigid framework. Various factors could have affected the ecological amplitude in the past, such as the climate characteristics. Therefore, we cannot exclude the possibility that trophic requirements of taxa could have been different. A list of preferences of peat species in terms of the substrate trophy was presented by Grosse-Brauckmann (1990), who assumed the possibility of a wider ecological amplitude of *Polytrichum strictum*, which may appear on the less acidic, more fertile mires. Under such conditions, this species could possibly meet with *Equisetum fluviatile*. However, the latter prefers richer substrate with higher pH values. Chee and Vitt (1989) noted *Equisetum fluviatile* in different types of fens in central Canada but not on bogs. Grosse-Brauckmann (1990) was more restrictive to peat mosses, like *Sphagnum magellanicum*, *S. fuscum* and *S. rubellum*, assigning them definitely to acid, poor substrates. Also according to Bragazaa *et al.* (2005), *S. fuscum* is typical for acid, poor substrates. While for *S. magellanicum*, this is not so obvious. Hassel *et al.* (2018), distinguish two species within the former *Sphagnum magellanicum*. The first of them — *S. medium* is connected with ombrotrophic bogs and the second one — *S. divinum* is a species of minerotrophic fens. This distinction might bear significance for correct interpretation of fossil record. It would also agree with the observations from Bragazza *et al.* (2005) in Sweden with *S. magellanicum* being present on minerotrophic lawns. The same applies to *Menyanthes trifoliata* and, in fact, trophic requirements of this species (trophic value is 3–4 according to Zarzycki *et al.* 2002) places it on less acid mires — richer than those typical for *S. magellanicum* (in the previous meaning) (Grosse-Brauckmann 1990). Vitt and Slack (1984) indicated that *S. fuscum*, *S. magelanicum* and *S. rubellum* occur on substratum with pH value less than 6, even 4.5 for *S. fuscum*, whereas *S. teres* is connected with pH value of about 7.6. According to Chee and Vitt (1989), the optimal conditions for *S. teres* are noted on moderate rich fens. This species belongs to the so-called calcitolerant peat mosses (Hájková and Hájek 2004). Regarding *S. palustre*, it grows in mesotrophic to eutrophic peatland habitats and it is absent in calcareous and bog environments (Temmink *et al.* 2017). Therefore, its coexistence with Ericaceae dwarf shrubs in the studied mire is quite unexpected. However, the lack of species recognition among Ericaceae extends possibility of such co-occurrence. For example, the presence of *Andromeda polifolia* could indicate poor, acid substrate, similar to now in Central Europe. On the other hand, this species grows along the whole pH gradient in the northern part of this continent. Also in the case of *Vaccinium oxycoccos*, the ecological range is wider (see Grosse-Brauckmann 1990). To a certain extent, this also applies to the coexistence of *Equisetum fluviatile* and peat mosses from the *Cuspidata* section. This section includes species such as *Sphagnum fallax*, *S. flexuosum*, *S. cuspidatum*, *S. angustifolium* or *S. majus*, which are bog species but their presence in poor fens is also noted (Chee and Vitt 1989). Therefore, there is the possibility of co-occurrence with *Equisetum fluviatile.*

Some examples of contemporary combinations of species similar to the, statistically significant and positive associations of *Sphagnum fuscum*/*rubellum-Carex* community at BIII have been reported. Peterka *et al.* (2015) noted such relevés mostly in northern Europe. Examples of such coexistences include *Sphagnum fuscum-Equisetum fluviatile* — in central and northern Finland; *Sphagnum rubellum-Equisetum fluviatile* — in central Norway; *Sphagnum fuscum-Sphagnum teres* — in northern Finland (Oulanka National Park), northern Sweden (also with *Phragmites australis* and *Sphagnum palustre*); *Polytrichum strictum-Equisetum fluviatile* — in northern Sweden and in the far north of Norway; *Polytrichum strictum-Sphagnum teres* — in southern Finland. Hence, such vegetation is rare, but it exists, more often in the north at the so-called mixed mires. These mires are specific ecosystems where minerotrophic and ombrotrophic structures alternate in one mire at small scale (Persson 1961). High hummocks of *Sphagnum rubellum* and *Sphagnum fuscum* are scattered throughout the minerotrophic fens building "miniature bogs" (Bellamy and Rieley 1967). Besides the boreal zone, mixed mires are also noted, but as small areas in the Carpathians (Hájková and Hájek 2004), in the Bulgarian mountains (Hájková *et al.* 2006) and in the Southern Alps (Marini *et al.* 2008). It shows that the trophic preferences of plants and their requirements for pH of the base can be less radical than we can assume based on the ecological numbers.

Concerning moisture preferences of taxa forming the *Sphagnum fuscum*/*rubellum*-*Carex* community, both fen species (*Equisetum fluviatile* and *Carex riparia*) and bog species (*Andromeda polifolia* and *Betula nana*) are connected with the wet substratum. Their soil moisture values are five according to Zarzycki *et al.* (2002), and nine to ten according to Ellenberg (1974) and Ellenberg *et al.* (1992). However, it is also possible to distinguish taxa with smaller and higher needs of humidity of the substratum. In the case of bog plants, moisture values reflect the location of species in relation to the gradient of the water table, so its position in the hummock-lawn-carpet-mud bottom-bog pools series (see Sjörs 1948). *Sphagnum fuscum*, *Polytrichum strictum* and *Sphagnum rubellum* are high and low hummock species at present, and they occur above the water table. For the two first mentioned species, Vitt and Slack (1984) indicated the position 40 cm above the water level. In the subfossil record, their presence is also interpreted as a sign of a lower ground water level (soil moisture value is six), whereas *Sphagnum teres* and *Equisetum fluviatile* are connected with a more humid substratum (soil moisture value is seven and ten, respectively) (see Elina and Yurkovskaya 1992, Drzymulska 2017). In our reconstructed *Sphagnum fuscum*/*rubellum*-*Carex* community, *Sphagnum fuscum*/*rubellum* and *Equisetum fluviatile*, *Polytrichum strictum* and *Equisetum fluviatile*, *Polytrichum strictum* and *Sphagnum teres*, *Sphagnum fuscum*/*rubellum* and *Sphagnum teres* showed positive co-occurrence (Fig. 4b). As discussed above on the overlap of ecological ranges of plant species, it is possible that hummock species, as being more resistant to moisture changes than hollow species (see Rydin and Jeglum 2008), can thrive even in fens. However, in this case, additional factors may contribute, such as the co-occurrence of the other peat moss species, specifically those that can actively reduce the pH of the substrate and thus facilitate the appearance of bog peat mosses (see Clymo and Hayward 1982). In conclusion, it cannot be ruled out that Borki mire was a poor fen that is relatively accessible for bog species.

The findings above indicate that the initial plant cover existing on the mineral ground at the Borki site cannot be easily defined from the vantage point of both contemporary and subfossil vegetation. It should therefore be asked how such atypical coexistence of species arise on the mires. Concerning the mixed mires mentioned above, the heterogeneity must result from the ability of various mosses to direct succession through acidification (Glime *et al.* 1982). While the pH-lowering ability of *Sphagnum* is well known (Clymo 1963, Soudzilovskaia *et al.* 2010), the same capability of non-*Sphagnum* mosses is less expected. However, such effect was confirmed for *Campylium stellatum* and *Drepanocladus revolvens*, both alkaline-tolerant species, which were able to lower the pH of marsh water in Lawrence Lake (Michigan) (Glime *et al.* 1982). In this way, the increase in acidity gives rise to the change of the moss species composition in peatlands towards the dominance of *Sphagnum* species. Along with the peat accumulation process, this is the reason for the more progressive separation of mire surfaces from the direct influence of mineral-rich groundwater. According to Vicherová *et al.* (2017), the important factors speeding up successional shifts towards poor fens also include the retained rainwater and hardly decomposable *Sphagnum* litter separating mire surface from groundwater. Is this scenario also attributable to the studied site, or does it rather mean that in the past, in the early Holocene, species were characterized by different trophy and pH substratum preferences from today? The increase in acidity can be accounted to specific water supply conditions characteristic for the studied mire at the beginning of the Holocene but with no direct equivalents in the present systems. It is possible that a flood terrace of the Sokołda River, neighbouring the plateau at present, was not yet formed in the Preboreal period. We know that nowadays the river valley cutting the deep water-bearing horizon causes the outflow of the artesian groundwater (Dembek 1989). The delayed development of the river valley in relation to the peat formation could have resulted in the hydrological conditions of the mire. Hence, these conditions were probably dependent on specific climatic factors causing a low groundwater table during the Younger Dryas and the Preboreal period (see Ralska-Jasiewiczowa and Starkel 1988), and this affected the development of the specific plant taxa combination. However, also other causes, like mire habitat or wider genetic diversity of species, may have been important. Therefore, the ecological niches of taxa in Central Europe could be different during the Late Glacial and the beginning of the Holocene than today.

Significant vegetation change at the studied mire started in the middle of the Boreal period. This could be associated with the alterations in the Sokołda River valley, which resulted in the onset of the water supply from the plateau into the mire. These changes, in turn, were probably triggered by heavy rainfall and a strong surface flow detected at this time in northern Poland (Ralska-Jasiewiczowa and Starkel 1988), leading to the transformation of river valleys (see Starkel 2005). Another vegetation change started in the first half of the Subboreal period, when the community of *Carex*-*Sphagnum* sect. *Sphagnum*-*Pinus* appeared. This community was characterized by a high proportion of *Pinus sylvestris*, *Carex* sp. and peat mosses from the *Sphagnum* section. This thicket community with oligotrophic elements, like *Sphagnum magellanicum*, could be connected with the periodic reduction of water supply from the plateau. Such subfossil phytocoenosis seems to be related to the contemporary Western Siberian pine-birch-sedge-peat moss communities (Liss and Bjeresina 1981) or to European community with sedge, pine and birch (*Schnabelseggen-Kiefern-Birkenwald*) (Ellenberg and Leuschner 2010), although, at the Borki mire, with a minor share of birch.

Conclusions

Based on the analysis of plant macrofossils, atypical subfossil phytocoenosis was recognized at one of the mires of NE Poland. It is difficult to categorise this phytocoenosis clearly with neither contemporary nor past known plant communities. Importantly, this composition of coexisting plant taxa was also statistically confirmed with significant, non-random, positive associations between some pairs of taxa found. The *Sphagnum fuscum*/*rubellum*-*Carex* community revealed that our previous understanding of subfossil vegetation should be evaluated. Therefore, the phytocoenoses that are rare at present and assigned to the northern regions could have existed at the beginning of the Holocene further to the south. The reason for such a condition in the Borki site was probably a consequence of specific hydrological conditions connected with the river valley development. Different climate and mire connectivity in the landscape, similar to current Fennoscandia cannot be ruled out either.

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